Life history of the flea beetle, *Argopistes coccinelliformis* Csiki (Coleoptera: Chrysomelidae) VII. Effects of photoperiod and temperature on induction of reproductive diapause in newly emerged adults

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**Abstract**
At 20°C, only 0–19% of newly emerged females of *Argopistes coccinelliformis* laid eggs under short-day conditions (LD 13.5 : 10.5, 13 : 11 and 12 : 12), but all females laid eggs within 30 days after emergence under long-day conditions (LD 14.5 : 9.5 and 15 : 9). The critical photoperiod was between LD 13.5 : 10.5 and 14 : 10. At 25°C, 27–39% of females laid eggs within 60 days after emergence even under short-day conditions (LD 12.5 : 11.5 and 12 : 12). All females laid eggs under long-day conditions (LD 14.5 : 9.5 and 15 : 9), but the preoviposition periods were longer than those at 20°C. The critical photoperiod was between LD 14 : 10 and 14.5 : 9.5 when it was estimated on the 20th day from emergence and between LD 12.5 : 11.5 and 13 : 11 when it was estimated on the 60th day. At 28°C, 41–73% of females laid eggs within 60 days after emergence under short-day conditions (LD 13 : 11, 12.5 : 11.5 and 12 : 12), but 14–33% of females did not lay eggs, even under long-day conditions. The critical photoperiod could not be determined. From the past and the present data, I concluded that *A. coccinelliformis* might produce 4 generations per year around Tokyo, central Japan, if new sprouts of host plants are available beyond the spring. The best season for trimming host plants would be late autumn–early winter to control the flea beetle population.

**Key words:** *Argopistes coccinelliformis*, diapause, critical photoperiod, temperature, voltinism

**INTRODUCTION**

*Argopistes coccinelliformis* Csiki is a common pest of Oleaceae. Overwintered females usually mate and lay eggs on new leaves of host trees, such as *Osmanthus* × *fortunei* in April–May, and new adults emerge in June–July in southern Kanto, central Japan (Inoue and Shinkaji, 1989). However, when lammas shoots (shoots which are produced after the spring) are produced on host trees during mid-summer and autumn, a small number of eggs are laid again, and a portion of these can develop into adults (Inoue and Shinkaji, 1989). It is believed that most eggs on lammas shoots are laid by surviving overwintered females (Inoue and Shinkaji, 1990). However, some newly-emerged females can oviposit when supplied with new leaves soon after emergence (Inoue, 1991). Thus, a few of the eggs found on lammas shoots during mid-summer and autumn may be laid by new adults. Inoue (1998) experimentally demonstrated that first and second generation adults can overwinter and produce offspring regardless of the emergence season. Furthermore, because a small portion of second generation females have been observed to lay eggs immediately after eclosion, a third generation might possibly be produced under field conditions (Inoue, 1998). Thus, this species is a facultative multivoltine.

In recent years, the trimming of ornamental trees is being conducted not only in winter, but also in late spring and/or summer. After trimming, many new shoots (lammas shoots) are usually produced. Inoue (1998) suggested that lammas shoot production after trimming conducted from late spring to early autumn promotes oviposition by surviving overwintered and newly-emerged adults, and as a result, trimming, a traditional management operation, may provide *A. coccinelliformis* with an opportunity to increase its population the following year, and to increase the number of generations.

Many temperate insects enter diapause in response to photoperiod (e.g. Danks, 1987). And the photoperiodic parameters for diapause induction can be incorporated into a photothermograph that relates the heat accumulation with seasonal change of day length and thus predicts the number of generations and the initiation of diapause for multivoltine species (Tauber et al., 1986). In a previous study, new adults of *A. coccinelliformis* could
oviposit under long photoperiod (LD 15:9) but not under short photoperiod (LD 12:12) (Inoue and Shinkaji, 1990). Namely, the diapause of new adults was induced by short photoperiod. Overwintered adults could oviposit even under short photoperiod (Inoue and Shinkaji, 1990). Those overwintered adults continued ovipositing under the long photoperiod, but diapause was again induced under the short photoperiod (Inoue and Shinkaji, 1990).

The developmental zero and the total effective temperature for development of immature stages in *A. coccinelliformis* have already been clarified (Tamura and Takeuchi, 1992). However, the critical photoperiods for diapause induction in new adults and for diapause re-induction in overwintered adults were not clarified in detail in past reports. Thus, since Inoue (1998) emphasized that it is necessary to determine these two critical photoperiods in order to predict the possible number of generations of *A. coccinelliformis* and to estimate the best season for trimming host plants, I undertook this study to determine the effects of photoperiod and temperature on induction of reproductive diapause in newly emerged *A. coccinelliformis* adults.

**MATERIALS AND METHODS**

Newly emerged adults were collected on the premises of the Forestry and Forest Products Research Institute, located in Kukizaki-machi, Ibaraki Prefecture, central Japan every June from 1996 to 1998. Plastic containers laid upside down on the surface of the ground under infected host trees were used as emergence traps. Adults were removed from the traps daily. Females were individually reared in glass cylinders (15 cm in length, 3 cm in dia.), which were placed in climate controlled chambers. They were supplied with new sprouts of *Osmanthus fragrans* var. *aurantiacus*, with stems wrapped in water-soaked absorbent cotton. Food was replenished every two days, at which time the oviposition was checked. Three different temperatures (20°C, 25°C or 28°C) and eight different photoperiods ranging from LD 12:12 to 16:8 were used for the rearing. Twenty rearing groups containing 21–31 females each were established (Figs. 1–3). The rearing of females was terminated on the 60th day. Several adults that had died without oviposition before 60 days from the start of the rearing were omitted from the analyses.

The developmental zero and the total effective temperature for development of all stages (egg to pupa) in the Tokyo population of *A. coccinelliformis* are 10.4°C and 440 day-degrees, respectively (Tamura and Takeuchi, 1992). To predict the possible number of generations around Tokyo, I used these values. The previposition period of each generation was estimated from the present study. The meteorological data (mean air temperature and day length from dawn to dusk) were taken from the “Chronological Scientific Tables 1999” (National Astronomical Observatory, 1998).

**RESULTS**

Effects of photoperiod and temperature on the induction of reproductive diapause in newly emerged adults

Photoperiodic responses at 20°C, 25°C and 28°C are shown in Figs. 1, 2 and 3, respectively. At 20°C, the photoperiodic response of females showed the long-day type, i.e., less than 20% of females kept under LD 13.5:10.5 or shorter photoregimes laid eggs within 60 days from emergence; however, more than 90% of females kept under photoregimes of LD 14:10 or longer laid eggs within 60 days from emergence (Fig. 1). Thus, the critical photoperiod for the induction of diapause was between LD 13.5:10.5 and 14:10.

At 25°C, 27–39% of females laid eggs within 60 days after emergence even under short photoregimes (LD 12:12 and 12.5:11.5). More than 90% of females kept under LD 14:10 or longer photoregimes laid eggs within 60 days from emergence; however, more than 90% of females kept under photoregimes of LD 14:10 or longer laid eggs within 30 days from emergence (Fig. 1). Thus, the critical photoperiod for the induction of diapause was between LD 13.5:10.5 and 14:10.

At 28°C, 41–73% of females laid eggs within 60 days after emergence even under short photoregimes (LD 12:12 and 12.5:11.5). More than 90% of females kept under LD 14:10 or longer photoregimes laid eggs within 60 days from emergence. All females laid eggs under LD 14.5:9.5 and 15:9 at 25°C, but the previposition periods were longer than those at 20°C (Fig. 2). The previposition periods (mean±SD) under LD 14.5:9.5 were 14.9±2.7 days at 20°C and 17.1±9.9 days at 25°C and those under LD 15:9 were 15.1±3.4 days at 20°C and 23.8±13.2 days at 25°C. The critical photoperiod was between LD 14:10 and 14.5:9.5 when it was estimated on the 20th day from emergence, but it was between LD 12.5:11.5 and 13:11 when it was estimated on the 60th day.

At 28°C, 41–73% of females kept under photoregimes of LD 13:11 or shorter laid eggs within 60 days after emergence. But 14–33°C of females
did not lay eggs even under photoregimes of LD 13.5 : 10.5 or longer (Fig. 3). The critical photoperiod was unclear, but if the data obtained under LD 12 : 12 are neglected, it was estimated to be between LD 13 : 11 and 13.5 : 10.5 (on the 60th day).

At 25°C, 4–19% of females kept under photoregimes of LD 14 : 10 or longer started to lay eggs after a very short preoviposition period (less than 10 days). Also, at 28°C, 5–29% of females kept under photoregimes of LD 12.5 : 11.5 or longer started to lay eggs within 10 days after emergence. The minimum preoviposition period at 25°C and 28°C was 8 and 6 days, respectively, but at 20°C, it was 12 days (Figs. 1–3).

**Prediction of the possible number of generations**

In the southern Kanto region, overwintered *A. coccinelliformis* usually start to lay eggs in mid-April (Inoue and Shinkaji, 1989; Tamura and Takeuchi, 1992). Thus, the present study was carried out assuming that the overwintered females started oviposition on 11 April. The shortest preoviposition period recorded under an experimental condition (temperature and daylength) most closely resembling the meteorological conditions on the date of emergence predicted in each generation was used for the calculation. Thus, the number of generations predicted in the present study is the maximum around Tokyo.

The predicted life cycle is shown in Fig. 4. Around Tokyo, four generations per year may possibly be produced under field conditions. The first generation adults may emerge in mid-June when the mean air temperature is a little higher than 20°C. The shortest preoviposition period of this generation was estimated to be 12 days from Fig. 1 (under LD 15 : 9), and thus females may start to lay eggs in late June. The second generation may occur in late July when the mean air temperature is between 25°C and 28°C. The shortest preoviposition period was 8 days and 6 days at 25°C and 28°C, respectively, when the daylength was longer than 15 h (Figs. 2 and 3). Thus, the preoviposition period of this generation was estimated to be 7 days, and females may start to lay eggs at the end of July. The third generation may occur in late August when the temperature is also between 25°C and 28°C and the daylength is between 14.5 h and 14 h. The preoviposition period of this generation was also estimated to be 7 days from Figs. 2 and 3, and
females may start to lay eggs at the beginning of September. The fourth generation adults may emerge in early October when the temperature is a little lower than 20°C and the daylength is between 13 h and 12.5 h. This may be the last generation because at 20°C, only a few females laid eggs after a long preoviposition period (more than 38 days) even under LD 13:11, and none laid eggs under LD 12:12 (Fig. 1).

**DISCUSSION**

**Effects of photoperiod and temperature on the induction of reproductive diapause in newly emerged adults**

Thermal alterations of the photoperiodic response have been recorded for many insect species. Generally, in long-day insects, low temperatures tend to promote diapause, whereas high temperatures tend to prevent it (e.g. Tauber et al., 1986). The photoperiodic response curves for the incidence of oviposition in *A. coccinelliformis* at different temperatures on the 30th day after emergence are shown in Fig. 5. In *A. coccinelliformis*, when the daylength was 13.5 h per day or shorter, higher temperatures (25°C and 28°C) tended to prevent diapause because higher percentages of oviposition incidence were recorded at these two temperatures than at 20°C (Fig. 5). This corresponds to the above generalization regarding the enhanced effect of low temperature on diapause. However, when the daylength was 14 h per day or longer, the role of temperature was the opposite—just like the thermal alterations of the photoperiod which have been recorded in short-day insects or insects that aestivate (Masaki, 1980). Namely, under longer photoregimes, higher temperatures tended to prevent oviposition because the percentage of oviposited females at 20°C was higher than at 25°C or 28°C (Fig. 5). Thus, the effect of photoperiod on the incidence of oviposition in *A. coccinelliformis* declined as the temperature rose from 20°C through 28°C.

A similar type of response was found in the dragonfly, *Plathemis lydia* (Shepard and Lutz, 1976). Diapausing larvae of this dragonfly were very sensitive to diapause-terminating long daylength at 15°C, but above 20°C the effect of long daylength declined. By this type of photoperiodic response, *P. lydia* can begin its larval maturation in spring while water temperatures are still low.
In this dragonfly, the growth rate of larvae under long daylength approaches that under short daylength as the temperature rises, but it does not fall below that under short daylength (Shepard and Lutz, 1976) as it does with *A. coccinelliformis*.

The feeding activity of *A. coccinelliformis* adults declines in summer (Inoue and Shinkaji, 1990), but the effects of temperature and/or photoperiod on the feeding activities are not known. The feeding activity of adults of the closely related species *A. biplagiatus* also declines in summer but increases again in autumn (Inoue, 1992). Because the amount of food consumption is greater under short photoregimes than under long photoregimes, it is believed that *A. biplagiatus* undergoes summer diapause (Inoue, 1993). Whether or not *A. coccinelliformis* adults are in a state of summer diapause during mid summer will be the subject of future studies.

*A. coccinelliformis* is found in Japan (Honshu, Shikoku, Kyushu, Hachijo-jima, Chichi-jima and Ryukyu Isls), Taiwan, S. China and Indo-China (Kimoto, 1965). Thus, *A. coccinelliformis* seems to have originated in the subtropical region (Asia), and the Kanto district of Japan seems to be its northernmost territory (Inoue and Shinkaji, 1990). Prior to an examination of the life cycle and the photoperiodic response in the subtropical population, discussions on the significance of the “intersecting” photoperiodic response of *A. coccinelliformis* demonstrated in the present study (Fig. 5) to the life history strategy of this insect may be premature. Nevertheless, the response observed under shorter photoregimes may enable adults to lay eggs later in the autumn in southern territories. Indeed, I observed young larvae of *A. coccinelliformis* during mid-November of 1999 on Ishigaki Island (24° 20’N) (Inoue, unpublished).

On the other hand, the mid-summer condition may lower the oviposition incidence in *A. coccinelliformis*. The incidence, however, is not completely suppressed because a considerable percentage of females laid eggs within a short period (10 or 20 days) after emergence and more than 60% of females laid eggs within 60 days after emergence at 25°C and 28°C under long photoregimes (Figs. 2 and 3).

In the southern territories, the response observed at higher temperatures may accommodate the gradual incidence of ovipositing individuals during summer and autumn, but in the northern territories, the percentage of females that overwinter before the start of oviposition may be greater than in the southern territories resulting from a drop in temperature and a shortening in daylength.

A trade-off between oviposition activity in the year of emergence and the overwintering success (and/or the oviposition activity in the following year) may exist. At least in Kochi, southwestern Japan, both females that had oviposited and that had not oviposited within the year of emergence could overwinter and lay eggs the following spring (Inoue, 1998). However, the relationship between the number of eggs laid in the year of emergence and that in the following year was not clarified in detail.

**Prediction of the possible number of generations and the best season for trimming**

Around Tokyo, four generations may possibly be produced under field conditions in one year (Fig. 4). Because females of *A. coccinelliformis* lay eggs only on new sprouts or new leaves (Inoue, 1991), the maximum number of generations may be realized when new leaves are produced continually on host trees even in summer and autumn; in the northern territories, this is only the case when the host trees are trimmed very frequently because most new shoots usually appear only once a year, that is in the spring. Inoue (1998) suggested that trimming should not be conducted from late spring to early autumn, but he did not specify the best season for trimming. From the present data, the last season that females can oviposit around Tokyo may be mid- to late September. Also, surviving overwintered females have been reported to cease laying eggs in mid-September in the field (Inoue and Shinkaji, 1990). Lammas shoots of host plants, such as *Osmanthus fragrans* var. *aurantiacus*, appear about 20–30 days after trimming (Inoue, 1998). Thus, trimming should not be conducted before mid- to late August, from the viewpoint of controlling *A. coccinelliformis* populations. Some host plant species of *A. coccinelliformis*, such as *Osmanthus* spp., flower in autumn. Therefore, the best season for trimming may be late autumn–early winter.
REFERENCES